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LAMELLORTHOCERATIDS (CEPHALOPODA,  
ORTHOCEROIDEA) FROM THE LOWER  
DEVONIAN OF NEW YORK<sup>1</sup>

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ABSTRACT

Devonian lamellorthoceratid cephalopods from North America are described in detail for the first time. They occur in the Esopus Shale of Emsian age of New York State and are here named *Esopoceras sinuosum*, gen. et sp. nov. They are straight, slowly expanding orthoconic forms characterized by cameral deposits in the form of sinuous, radiating lamellae, disposed in a unique geometric pattern. These internal lamellae fill all the chambers of the phragmocone of the holotype but appear to be absent from the body chamber. In cross section, these cephalopods bear some superficial resemblance to rugose corals.

The new species shows considerable variation in internal and external morphologic characters, which may be attributed to mode of preservation as well as to presence of different growth stages. *Esopoceras* resembles all of the four previously named genera comprising the family Lamellorthoceratidae, occurring in Europe, North Africa, Turkey, and the Urals, but it is most similar to the genus *Lamellorthoceras* (Termier and Termier, 1950). The existence of *Esopoceras* in North America greatly extends the geographic range of this short-lived and as yet little-known group of cephalopods.

INTRODUCTION AND ACKNOWLEDGMENTS

The family Lamellorthoceratidae is composed of a small group of genera having orthoconic shells characterized by cameral deposits in the form of more or less closely set, radiating lamellae spaced between successive septa, either vertically

or at various angles. Until recently members of this family were known only from rocks of Early and Middle Devonian (Siegenian to Couvinian) age of Europe (France, Germany, Ural Mountains), Turkey, and North Africa.

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In April, 1974, Mrs. Judith Rehmer Hepburn, Clark University, Worcester, Massachusetts, sent Curt Teichert a small collection of orthoconic cephalopods, which she had correctly identified as belonging to the family Lamellorthoceratidae. They were derived from the middle member of the Esopus Formation of Emsian age in a quarry near Rosendale in southern New York State.

After the manuscript of this paper had been almost completed we learned from Dr. R. H. Flower, New Mexico Bureau of Mines and Mineral Resources, that for some time he had had in his possession a collection of fossils made by Stephen Mellendorf, apparently from the same locality as Mrs. Hepburn's collection, and which also included representatives of Lamellorthoceratidae.

A preliminary note on this occurrence is under preparation by Flower and Mellendorf.

We are greatly indebted to Mrs. Hepburn for allowing us to describe this interesting and unusual group of orthocerid cephalopods, and we are grateful to Dr. Flower for a copy of his joint manuscript with Mellendorf. We are also indebted to Dr. Flower for bringing to our attention the paper by Howell (1942). Michael Frederick prepared the photographs of all New York specimens on Plates 1 and 2, and Roger B. Williams skillfully drafted the text-figures.

G. D. Stanley acknowledges support by the Wallace E. Pratt Research Fund at the University of Kansas. The Department of Geology at Princeton University generously loaned us the specimens illustrated by Howell (1942).

## DISTRIBUTION AND CHARACTERS OF LAMELLORTHOCERATIDAE

The family Lamellorthoceratidae was erected by Teichert (1961) to include *Arthrophyllum* Beyrich and *Lamellorthoceras* Termier and Termier, two genera of straight to slightly endogastric orthocerid cephalopods characterized by radiating cameral lamellae that, in some forms, almost completely fill the camerae of the phragmocone. In the *Treatise on Invertebrate Paleontology*, Sweet (in Teichert *et al.*, 1964) included in this family three genera, *Lamellorthoceras*, *Arthrophyllum*, and *Gorgonoceras* Zhuravleva. A fourth genus, *Coralloceras* Zhuravleva, considered by Sweet (in Teichert *et al.*, 1964, p. K234) to be synonymous with *Lamellorthoceras*, is regarded as a valid genus by us. The radiating cameral lamellae that characterize the members of this family superficially resemble the septa of rugose corals, and it is due to this remarkable convergence that Beyrich (in Carnall, Ewald, and Roth, 1850) named the first lamellorthoceratid *Arthrophyllum*, believing it to be a coral. A similar erroneous assignment of another lamellorthoceratid was later made by E. C. Stumm (in Howell, 1942; see below).

Almost all of the literature on this unique group of cephalopods is found in German, French,

and Russian publications. Of the four genera, *Arthrophyllum* occurs in Germany, *Gorgonoceras* in the Ural Mountains, *Coralloceras* in North Africa (Morocco, Algeria), and *Lamellorthoceras* in North Africa (Morocco, Algeria), Germany, France, and Turkey. *Esopoceras sinuosum* Stanley and Teichert, gen. et sp. nov., described in this paper, is from New York, and this discovery extends the range of this family to include eastern North America. The geologic range of Lamellorthoceratidae is relatively restricted within the Devonian, the family occurring in the Siegenian, Emsian, and Couvinian stages (upper Lower to lower Middle Devonian).

Except *Gorgonoceras*, which appears to be more distinct, the four genera share many characteristics, particularly in regard to the cameral deposits. Babin (1964) has already pointed out these similarities. Based on published descriptions and photographs available to us, we have assembled in Table 1 a comparison of the characters of the four previously described genera with those of the new genus *Esopoceras*, described herein.

The cameral lamellae that characterize the family vary in two respects: their configuration

TABLE 1. *Comparisons of Genera of Lamellorthoceratidae.*

	<i>Arthrophyllum</i>	<i>Coralloceras</i>	<i>Gorgonoceras</i>	<i>Lamellorthocerat</i>	<i>Esopoceras</i>
conch	laterally compressed	dorsoventrally depressed	circular	circular	circular and laterally compressed
ornament	?transverse crenulations	?	longitudinal costules	?fine, transverse-oblique striae	Longitudinal costules and smooth transverse annulations
sutures	straight	straight-oblique	straight-sl. oblique	undulating	undulating
posterior fissure	present	distinct	absent	present	?present
apical angle	Moderate (8-13°)	large (15-24°)	small (4°)	moderate (9-12°)	small (4-5°)
septa	slightly concave	moderately concave	strongly concave	strongly concave	strongly concave
Length/Width ratio of camerae	1:6-1:4	1:4-1:3	1:1-1:1.5	1:3-1:2	1:3-1:2
cameral deposits	episeptal only, nearly straight	episeptal only, ?nearly straight	epi- and hyposeptal; nearly straight to undulating	epi- and hyposeptal; nearly straight to undulating and curved	epi- and hyposeptal, nearly straight to highly undulating and slightly to strongly folded
geometry of external edges of lamellae	straight to slightly sinuous	straight to slightly sinuous	?straight	slightly sinuous, converge along transverse axis	slightly to highly sinuous, converge along transverse axis
Age	Emsian-Couvinian	Emsian-Couvinian	Couvinian	Siegenian-Couvinian	Emsian
Occurrence	Germany	North Africa	Urals	North Africa, Germany, Turkey, France	New York

in the camerae as they converge from the wall toward the siphuncle, and the shape of their external edges, which are in contact with the shell wall. The latter are apparent on steinkerns and are only an outward expression of the internal arrangement of the lamellae. The disposition and arrangement of the lamellae is a useful taxonomic character. Often, characters such as the position

of the siphuncle, apical angle, length/width ratio of chambers, and ornament are either too variable or difficult to ascertain due to poor preservation. Specimens that occur in dark shales are frequently crushed and replaced with iron sulfide that then converts to limonite, thus destroying most of the wall structures as well as obscuring the internal structures.

## PRESENT INVESTIGATIONS

Mrs. Judith Rehmer Hepburn made available to us a collection of about 13 specimens of straight cephalopods, which we describe here as *Esopoceras sinuosum* Stanley and Teichert, n. gen., n. sp. This collection came from the upper part of the middle member of the Esopus Formation (see Fenner, 1971, p. 16) at a quarry 1.2 km west of Cottekill, northwest of Rosendale, New York (Fig. 1). Cephalopods are restricted to the upper part of the middle member, which here consists

of uniform, homogeneous, dark, cherty, silty shale with clay and ironstone concretions. In addition to cephalopods the beds contain abundant brachiopods, rare gastropods, trace fossils, and plant remains (Judith Rehmer Hepburn, written commun., August, 1975).

The fossiliferous unit that contains the cephalopod fauna is 4.5 m thick. All cephalopods examined by us have orthoconic shells and are more or less fragmentary. This unit also contains other

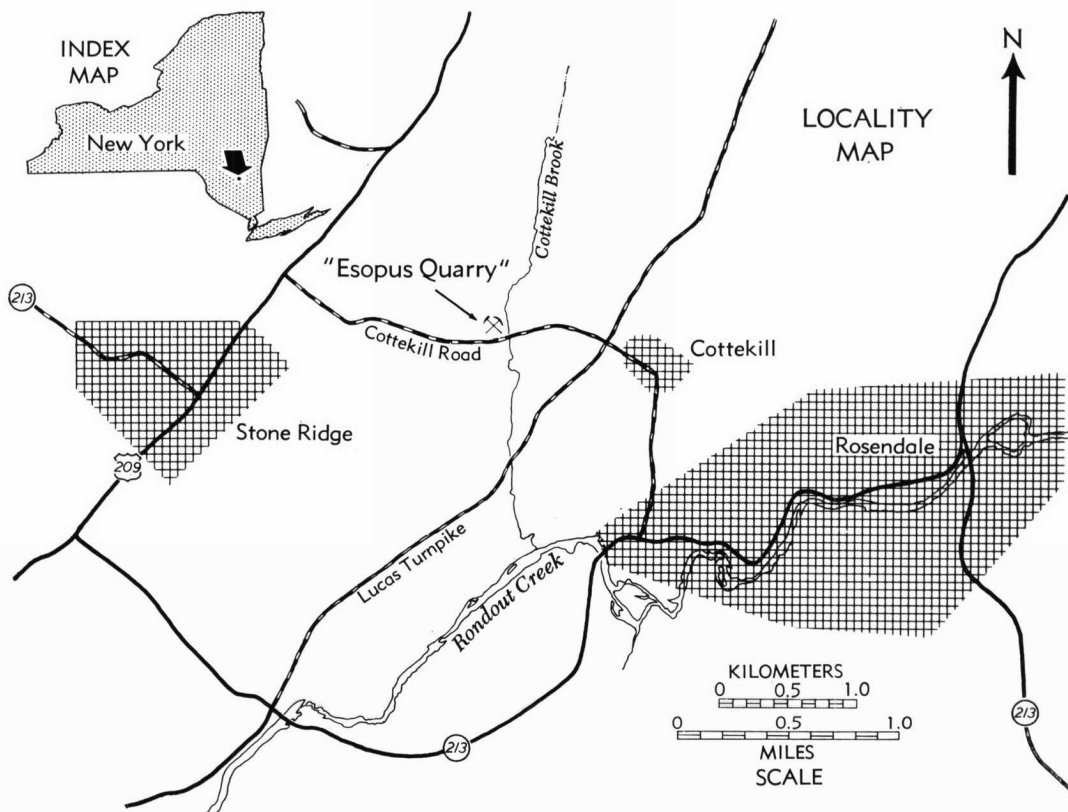


FIG. 1. Index map showing location of quarry in Esopus Formation from which *Esopoceras sinuosum* Stanley and Teichert, n. gen., n. sp., was obtained.

orthoconic cephalopods, the majority of which are either crushed or entirely flattened. This fact combined with their poor state of preservation, largely precludes positive identifications. It is significant to note, however, that none of the crushed or flattened shells yielded any signs of

the radiating cameral deposits that characterize *Esopoceras sinuosum*. This observation gives some credence to the possibility that the cameral deposits may have functioned to provide strength to the shell and thus prevent it from being crushed.

## SYSTEMATIC AND MORPHOLOGIC DESCRIPTION

### Class CEPHALOPODA Cuvier, 1798

#### Subclass ORTHOCERATOIDEA

H. Schmidt, 1935

[*nom. et correct. transl.* Teichert, 1967, p. 205, ex suborder Orthoceracea Kuhn, 1940, p. 18 (*recte* H. Schmidt, 1935, p. 59).]

### Order ORTHOCERIDA H. Schmidt, 1935

[*nom. correct. et transl.* Sweet in Teichert *et al.*, 1964, p. 223, ex suborder Orthoceracea Kuhn, 1940, p. 18 (*recte* H. Schmidt, 1935, p. 59).]

### Superfamily ORTHOCERATACEAE

Stokes, 1840

[*nom. correct. et transl.* Sweet, in Teichert *et al.*, 1964, p. 224, ex family Orthoceratidae M'Coy, 1844 (*recte* Orthocerata Stokes, 1840, p. 707).]

### Family LAMELLORTHOCERATIDAE

Teichert, 1961

### Genus ESOPOCERAS Stanley & Teichert, new

*Type species.*—*Esopoceras sinuosum* Stanley & Teichert, n. sp.



**Diagnosis.**—Straight, slowly expanding, nearly cylindrical conchs with circular to slightly compressed cross section; apical angle about four to five degrees; surface with annulations that correspond in position to the sutures. Three distinct shell layers are present, a thin, inner layer bears fine costules on external side; slight ?ventral depression present in earlier camerae of some specimens; sutures with broad saddles and lobes. Siphuncle near central; septa strongly concave; cameral deposits consist of radiating, straight to sinuous and curved lamellae that converge toward the siphuncle from the walls; both episeptal and hyposeptal deposits present; external edges of lamellae slightly to highly sinuous, showing bilateral symmetry with respect to dorsoventral and longitudinal axes.

**ESOPOCERAS SINUOSUM** Stanley & Teichert, n. sp.

Plate 1, figures 1-9, 13; Plate 2, figures 1, 4-9

*Zaphrentis* cf. *tabulata* Hall, Howell, 1942, p. 88, fig. 15, 1, 2.

**Diagnosis.**—Same as for genus.

## GENERAL MORPHOLOGY

**Shell features.**—The holotype (KUMIP 111622) is the steinkern of a straight, moderately expanding conch, which is 70 mm long (Pl. 1, fig. 6, 13). Its cross section is nearly circular near the anterior end, where the long and short diameters are 8 mm and 9 mm, respectively. The apical angle of the conch is estimated to be 6 or 7 degrees. The phragmocone contains 16 camerae, but an apical portion estimated to be 15-20 mm long is missing. The anterior end of the conch is somewhat crushed and almost certainly represents at least part of the body chamber, because no septa can be detected in it. This part is 12 mm long and flaring adorally. A paratype (KUMIP 111626) has a very slightly curved conch, but this is exceptional.

Since the siphuncle is nearly central and due to the absence of external shell features, it is impossible in the holotype and most other specimens to distinguish the ventral from the dorsal side. Somewhat arbitrarily, we are designating as the ventral side that margin along which the cameral lamellae (discussed below) converge (see Pl. 1, fig. 7, 8).

The conch of the holotype shows a very slight

?dorsal flattening and a depression in the internal mold of the apical portion. This is present on the first three preserved camerae and consists of a flattened area, which toward the posterior develops into a slight depression. The depression is absent adorally from the third camera. The loss of this external feature appears to coincide with a change in the cross-sectional shape from laterally compressed to more nearly circular. Just how the siphuncle position varies in relationship to those changes cannot be ascertained. Another specimen (KUMIP 111627) of comparable size shows a similar ?dorsal flattening.

The exterior of the holotype is weathered and poorly preserved, and most of the original shell wall has been removed. On parts of the surface of the steinkern low annulations seem to parallel the sutures. In places where the conch is more highly weathered, straight to somewhat sinuous, longitudinal lamellae appear on the outside of the steinkern. These are discussed in greater detail below.

The camerae have an average length of about 4 mm, and the ratio between the length of the camerae and their diameter varies from one-half to one-third. The curvature of the septa cannot be determined in the holotype, but in a paratype (KUMIP 111634), it can be seen that the septa are practically hemispherical (Pl. 1, fig. 1, 2). The siphuncle is narrow and central to subcentral in position. The preservation of the holotype as well as of all other specimens is such that features of the septal necks and connecting rings cannot be observed, except in a poorly preserved specimen (KUMIP 111632) which in polished cross section shows the conch to be circular with a subcentral siphuncle. The siphuncle shows a distinct, internal, ring-like lining resembling a connecting ring (Pl. 2, fig. 1). The exact nature of this feature is not discernible although it may be a kind of endosiphuncular deposit. In one well-preserved single camera (KUMIP 111626) that has a diameter of 8.0 mm, the diameter of the siphuncle is 1.0 mm.

From a study of all specimens, we conclude that three wall layers are present. These consist of an outer annulated layer, a middle longitudinally smooth layer, and an inner costulated layer. In specimen KUMIP 111623, two separate layers veneer the exterior surface of the sinuous lamellae. The first of these layers has straight longitudinal

costules, which are overlain by a smooth layer. The relationships between the sinuous lamellae and the longitudinally ornamented layer are well preserved in a partially crushed portion of a phragmocone having three camerae (KUMIP 111623) (Pl. 2, fig. 6). Approximately 10-12 costules occur here in 5 mm of conch circumference. The sinuous lamellae are faintly visible below the longitudinally ornamented veneer.

*Cameral deposits.*—In the holotype as well as many other specimens the camerae are filled with cameral deposits in the form of radiating lamellae that converge from the shell wall toward the siphuncle (Pl. 1, fig. 6). The 14th chamber of the holotype reveals an excellent three-dimensional view of the approximately 50 lamellae present. At the ?ventral side of the shell, the radiating lamellae near the periphery of the camerae are straight or only slightly sinuous and are oriented longitudinally. As the cameral lamellae approach the ?dorsal side of the chamber they become progressively more curved toward that side, where they assume an orientation more transverse to the conch (Pl. 1, fig. 6; Pl. 2, fig. 7). Another specimen (KUMIP 111624) also reveals an excellent three-dimensional view of similarly arranged lamellae (Pl. 1, fig. 7-9). Characteristically, each individual lamella is double layered. The layers are generally parallel and, approaching the wall, are joined together to form a loop at the junction with the succeeding septum (Pl. 1, fig. 3).

Although the holotype has a poorly preserved surface, two other specimens exhibit excellently the sinuous lamellae on the weathered surface. One of these (KUMIP 111626) is a well-preserved steinkern consisting of seven camerae (Pl. 1, fig. 3). The exterior surface is weathered and the surfaces of four camerae reveal the outer edges of sinuous, twisted lamellae between the sutures. Although the original shell wall appears to have been removed by weathering, faint, straight longitudinal ribs can be observed on the posterior portion. These riblike features appear to veneer the lamellae. Approximately 12 ribs occur per 5 mm of circumference.

On the surface of the steinkerns each lamella is approximately 0.2 mm wide and each is uniform in thickness along its length. Some lamellae are nearly straight or only slightly curved and traverse the full length between the sutures. At

an area on the ?dorsal side, the lamellae are highly curved, some to such an extent that they appear to be recumbently folded (Pl. 1, fig. 7,8). Although at first glance the external edges of the lamellae seem to be randomly sinuous, a detailed examination of two well-preserved specimens (KUMIP 111624 and 111626) as well as a clay impression of specimen 111624 reveals that the lamellae are grouped in two distinct sectors, one containing generally straight or only slightly sinuous lamellae and another displaying strongly sinuous, often recumbently folded, lamellae which converge anteriorly (Pl. 1, fig. 8).

The contacts between these sectors are rather gradational, and we arbitrarily assume that the region of highly folded converging lamellae corresponds to the ventral side of the conch. The disposition and arrangement of the lamellae on the weathered surface of the steinkern as well as the bilateral symmetry produced by the lamellae on the ?ventral side of the conch are an expression of the internal geometry of the cameral deposits.

On the weathered surface of the steinkern (KUMIP 111626), the edges of most lamellae are distinct and parallel. Some, however, occur in groups of two or three and coalesce in an adoral direction to form a single lamella (Pl. 1, fig. 9). This junction occurs approximately 0.5 mm from the most adapical suture of the succeeding chamber and produces an outward appearance of dendritic branching toward the posterior.

Another specimen (KUMIP 111624) is in a similar state of preservation although more weathered (Pl. 1, fig. 7-9). In some respects it illustrates the characteristic folding and convergence of the lamellae better than the previously described specimen KUMIP 111626. Specimen KUMIP 111624 is a phragmocone, 25 mm long, containing eight chambers all of which show externally sinuous lamellae. Plate 1, figure 8 shows the surface of a rolled-out clay impression of specimen (KUMIP 111624) illustrating the lamellae of the surface. In addition, this impression shows that the sutures each have a broad saddle and lobe. This undulation can also be seen in specimen KUMIP 111634 (Pl. 1, fig. 1,2), which is a single camera. Specimen KUMIP 111624 has portions of the surface in the posterior region excavated by weathering. Here, lamellae

are straight or only slightly sinuous on the surface (Plate 1, fig. 9). These sinuous lamellae can also be seen on weathered portions of the wall of specimen KUMIP 111634 (Pl. 1, fig. 1).

The cameral deposits are especially characteristic and are readily apparent in most of the specimens as well as in polished cross sections. They have been previously mentioned in the description of the holotype but their presence in polished transverse sections warrants further description.

*Polished cross sections.*—KUMIP 111632 is a polished circular cross section of a conch 7 mm in diameter. The cameral deposits are radiating lamellae, some of which appear to coalesce to some degree and merge with adjacent deposits (Pl. 2, fig. 1,4,5,9). Both episepal and hyposepal deposits can be seen. An oblique view of a conch with a circular diameter of 8 mm (KUMIP 111626), shows similar radiating lamellae, especially toward the periphery of the conch (Pl. 1, fig. 3).

KUMIP 111633 is a polished cross section of the phragmocone of a slightly larger specimen with short and long diameters of 8 mm and 12.5 mm. In this specimen the lamellae are fairly straight in the ?ventral portion of the camerae but those in the opposite, ?dorsal, portion are recurved toward the ?dorsal side (Pl. 2, fig. 7). The same orientation of the lamellae can also be seen in another cross section (KUMIP 111631) in which approximately 50 to 60 lamellae are present.

Under microscopic examination, individual double-layered lamellae can be observed to separate in the proximity of the inner shell wall and then converge at their termination (Pl. 2, fig. 5,8,9; Pl. 1, fig. 4). This condition is seen in specimen KUMIP 111633 at 0.3 to 0.4 mm from the shell wall. Another cross section (KUMIP 111623) is partially crushed but also appears to be compressed, having long and short diameters of 12 and 9 mm. The exterior of this specimen appears to retain some original wall structure as has been described above. The cameral deposits appear similar to those of the previously described cross section (KUMIP 111633), although some of the central area is obscured.

A slightly tangential polished cross section, made from one well-preserved specimen (KUMIP 111623, see Pl. 2, fig. 6), reveals the nature of the contact between the lamellae and the inner

wall. Although the center of this cross section is obscure due to replacement, much detail around the periphery is preserved. Microscopic examination of this specimen at low magnification in reflected light reveals considerable detail (Pl. 1, fig. 4). Some of the finer features of the lamellae observed in a cross section (KUMIP 111633) are the following:

Straight to slightly sinuous lamellae radiate from a near central siphuncle (Pl. 2, fig. 1). The sinuous lamellae consist of two laminae which are nearly parallel. At some points along their length, however, the double lamellae are in contact. The lamellae join together toward the periphery of the conch near the shell wall to produce a "double loop" appearance (Pl. 1, fig. 4). This can also be observed in some of the specimens with well-preserved interiors (KUMIP 111622, 111626, 111628). Specimen 111626 is illustrated in Plate 1, figure 3.

Another polished cross section, KUMIP 111630, well illustrates the presence of episepal as well as hyposepal deposits (Pl. 2, fig. 5,9). Due to the fact that the areas between the lamellae are replaced with clear, transparent calcite, the lamellae can be seen in three-dimensional view to be wavy and sinuous. Near the intersection with a septum in a two-dimensional plane, such as in the plane of the thin section, they may appear to be straight. The thickness of a pair of looped lamellae is highly variable, ranging between 0.1 mm and 0.5 mm while individual lamellae of a pair in a loop range in width between 0.05 and 0.3 mm. Most paired lamellae making up a single cameral deposit are approximately 0.1 mm wide (Pl. 2, fig. 9).

One portion of the sectioned conch of specimen 111623 is irregularly weathered around the periphery and shows some inner wall structures, 0.37-0.43 mm thick (Pl. 1, fig. 4). This wall structure is largely oxidized to limonitic material, but the contact with the inner lamellae is distinct. Toward the periphery of the specimen, the individual lamellae are tightly packed and bifurcate terminally, creating a forked appearance, with the terminus of each fork extending into the wall structure within a chamber at the contact with the wall (Pl. 1, fig. 4). This can also be seen in another thin section (Pl. 2, fig. 8). Some of the bifurcated terminal lamellae are slightly sinuous whereas others are straight. Most

appear to narrow appreciably toward the wall. The length of a lamella measured from where it bifurcates to the point at which it meets the wall is approximately 0.2 mm.

In specimens where the longitudinal, costulate wall structures are preserved (Pl. 2, fig. 6), transverse cross sections show that the terminal end of every other lamella occupies a position directly adjacent to a costule and each intervening lamella occupies the low area of furrow between the costules (Pl. 1, fig. 4). Such a correspondence occurs only where the lamellae are relatively straight. Due to the poor preservation of the material, details of the wall structure cannot always be ascertained. In another transverse section (KUMIP 111633), the thin terminals of the bifurcated lamellae are drawn out very finely and are highly sinuous (Pl. 2, fig. 8). They eventually become curved and meet the wall tangentially rather than terminating against it as described in KUMIP 111623. In specimen KUMIP 111623, the outer wall itself and the extending costules appear to be filled with yellowish-orange, laminated, limonitic material which, in some places, is draped over the costules (Pl. 1, fig. 4). This limonitic material is approximately 0.05 mm thick and covers the outer surface of the specimen. Depending on the degree of surface weathering, this coating overlies either the costulated wall or the sinuous lamellae. As seen in cross section (specimen KUMIP 111623), the individual costules are 0.15-0.3 mm thick and, depending on the degree of weathering, rise from 0.2 to 0.4 mm above the base of the inner wall (Pl. 1, fig. 4).

## DISCUSSIONS AND COMPARISONS

*Variations within the species.*—The lamellorhynchoceratids from New York are strikingly variable not only from specimen to specimen, but also within a single specimen. Variations are evident in the shape of the conch, especially in cross section, but considerable variation is also evident in the position of the siphuncle and in the disposition of the radiating cameral deposits. A detailed study of several well-preserved phragmocones, as well as polished cross sections, has shown that these variations are a function of quality of preservation and relative position of a particular fragment within the phragmocone. Presumably some variation is also attributable to the age of

the specimen to which the phragmocone belongs. Aside from the inherent effects of diagenetic alteration and weathering, considerable variations along the length of the conch are evident. This is best shown in the holotype (KUMIP 111622), but unfortunately, much of the finer features of the exterior surface are lost due to poor preservation.

The holotype is the longest and most complete specimen and also appears to possess a portion of the living chamber. Remarkably, in this specimen all camerae contain cameral lamellae deposits, which is in marked contrast to the condition found in other orthoconic cephalopods in which cameral deposits are weak or absent in the youngest camerae of the phragmocone (Flower, 1955; Teichert *et al.*, 1964; Fischer and Teichert, 1969).

Other notable variations consist of changes in the cross-sectional shape. This is apparent in other specimens as well as the holotype in which, unfortunately, about three to four centimeters of the apical portion are missing. In the holotype (KUMIP 111622), the most adapical portion of the phragmocone is almost circular in cross section at diameters of 6 to 8 mm. The shape of the cross section subsequently changes after the first two camerae to assume a slightly compressed shape; this again changes to a circular shape in the last few camerae. It is difficult to assess just how much of this variation is due to deformation. Although the changes from circular to compressed are highly unusual for orthoconic cephalopods, a similar sequence seems to be present at approximately the same position in other specimens.

A ?dorsal depression is another possible morphologic variation of the conch. It occurs in the smallest, circular portions of two specimens and, in the holotype, seems to disappear at the place where the change in cross-sectional shape from circular to compressed takes place.

The sinuosity of the outer edges of the lamellae that characterizes the exterior of the holotype, as well as of some paratypes, is distinctive. Variations of the exterior exclude sinuous lamellae, longitudinally striated costules, smooth, unornamented surfaces, and a surface characterized by gross annulations corresponding to the sutures. These features are diagrammatically depicted in Figure 2. Variations in surface



features, in our opinion, can be attributed to varying degrees of weathering. A careful study of all the specimens and their surface ornament has shown the presence of two, or possibly three, wall layers, each possessing different characters. These are first, a longitudinally ribbed (costulate) layer (KUMIP 111634 and 111624) resting directly on the edges of the sinuous lamellae and, second, an overlying smooth, unornamented layer (111634), and possibly a third layer with an annulated surface (Pl. 1, fig. 5). This last layer is perceptible in the holotype but due to poor preservation, its details cannot be clearly seen. Thus, depending on the degree of weathering, specimens can display any of the above surface ornaments.

The most intriguing characteristics of *Esopoceras sinuosum* are the internal cameral deposits, referred to as cameral lamellae. These deposits are believed to have considerable taxonomic value, but they also show great variation in symmetry and orientation. In cross section, both radial and bilateral symmetry are evident. A close study

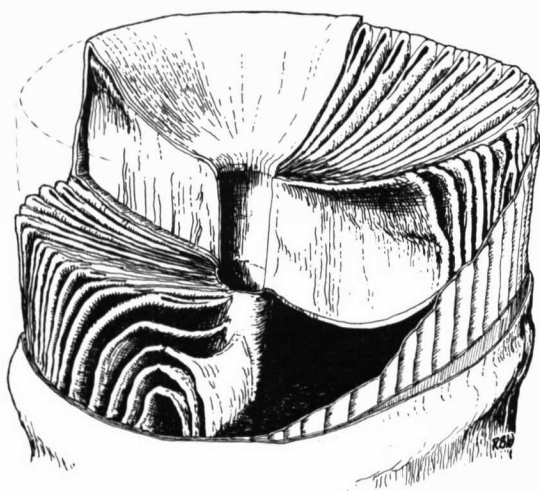


FIG. 2. *Esopoceras sinuosum* Stanley & Teichert, n. gen., n. sp. Diagrammatic representation of the double-layered cameral lamellae showing differently exposed views in two chambers. One-fourth of the cameral deposits in the lower right chamber as well as half of those in the upper chamber are not shown; drawing is based on morphologic features observed in several specimens and illustrates the manner in which the radiating cameral lamellae become progressively curved about the longitudinal axis of the shell. The three wall layers depicted on the right are discussed in text.

of these cameral deposits in a variety of differentially weathered and broken specimens as well as polished cross sections has revealed considerable detail concerning their disposition and orientation. This is illustrated diagrammatically in Figure 2. Since there is much variation within camerae, the appearance of radial versus bilateral symmetry in cross sections appears to be dependent on the position of the section within a camera. In some cross sections studied, the cameral deposits have been observed to change their orientation from the longitudinal to a transverse plane. This change is particularly evident in the larger camerae and occurs approximately in their middle. It occurs in a progressive manner toward the ?dorsal side where relatively straight, longitudinal, cameral deposits gradually assume an orientation more parallel to the septa. At the junction with the succeeding septa, however, they change rapidly, reverting to their former longitudinal, radial arrangement. Since the average camerae are only about 3 or 4 mm long, this change occurs within a relatively short distance. In cross sections, within portions of the camerae where the cameral deposits are strongly inclined to the transverse plane, the cameral lamellae appear to be progressively curved toward the ?ventral side (Pl. 1, fig. 6; Pl. 2, fig. 7), thus producing bilateral symmetry. On the other hand, where the cameral lamellae are straight and longitudinally oriented, a distinct radially symmetrical pattern results (Pl. 2, fig. 1). Thus, the position of a cross section within a chamber determines whether it appears to be radial or bilateral in symmetry. In addition, this bilateral symmetry becomes markedly apparent in the larger, more proximal camerae.

The external, wavy lamellae that characterize the exterior of many steinkerns are the outer edges of the cameral deposits. The progressive change from relatively straight to highly twisted and folded outline (Pl. 1, fig. 7-9), corresponds to the progressive change in the orientation of the internal cameral deposits. In external view, the sinuous and folded external lamellae always return to a nearly longitudinal orientation where they meet the next septum (Pl. 1, fig. 7-9).

Another curious feature of the cameral deposits are the strongly curved and often connected structures that surround the siphuncle (Pl. 2, fig. 4,7). Some of these are semicircular

in cross section. They resemble circuli as illustrated and described by Fischer and Teichert (1969). They differ from the radiating cameral deposits primarily by having a different orientation and also by being connected and therefore presumably arising from the siphuncle rather than the wall.

**Occurrence.**—Esopus Shale (Emsian) of New York at a quarry near Rosendale, New York. The specimens occur in pyritized shale with brachiopods and other orthoconic cephalopods.

**Repository.**—Holotype KUMIP 111622, paratypes KUMIP 111623-111634, University of Kansas Museum of Invertebrate Paleontology, Lawrence, Kansas.

**External resemblance to corals.**—As previously mentioned, the radiating, lamellar, cameral deposits which characterize the cephalopod *Arthrophyllum* in Germany, originally led Beyrich (in Carnall *et al.*, 1850) to conclude that this fossil is a coral. A similar misidentification was later made in North America when E. C. Stumm (in Howell, 1942) identified some fossils from the Esopus Shale of New York State as "*Zaphrentis cf. tabulata* Hall."

We have examined the two specimens figured by Howell (1942) and find them to be orthoconic cephalopods and not rugose corals. They are both almost completely replaced by marcasite and are in such poor state of preservation as to preclude positive identification. The presence of vague traces of sinuous external lamellae, similar to those of *Esopoceras sinuosum*, as well as nearly identical dimensions of the conch suggest that the specimens illustrated by Howell do indeed belong to *E. sinuosum*. This contention is supported further by the fact that the locality information for Howell's specimens indicates that they may have been collected from the very same quarry that yielded the specimens we describe herein.

**Comparisons with other lamellorthoceratid genera.**—*Esopoceras* bears some resemblances to other lamellorthoceratid genera. It appears to be most similar to *Lamellorthoceras* (Termier and Termier, 1950), described from the Eifelian of Morocco, with *L. vermiculare* as type species. In many respects *Esopoceras* also shows features similar to two other genera, *Corallocceras* (Zhuravleva, in Ruzhentsev, 1962) and *Arthrophyllum* (Beyrich, in Carnall *et al.*, 1850). The type species

of *Corallocceras* was first described by Le Maitre (1950) as *Orthoceras coralliforme*, and that of *Arthrophyllum*, as *Orthoceras crassum* Roemer (1843), later designated as type species by Roemer (1852).

Teichert (1961) restudied the original specimens of *Lamellorthoceras vermiculare* Termier and Termier (1950), compared them with *Arthrophyllum*, and presented an historical account of both generic concepts. *L. vermiculare* has some features in common with *Esopoceras sinuosum*, such as dimensions of the camerae and structure of cameral deposits. The most striking resemblance between these two species lies in the sinuosity of the lamellae on the surface of steinkerns and also in the interior of the camerae. Plate 1, figures 10 and 11, and Plate 2, figures 2 and 3, are illustrations of external views and cross sections of *L. vermiculare*, four of which were previously figured by Teichert (1961, pl. 1, fig. 11,12; pl. 2, fig. 10,12). The strong sinuosity of the cameral lamellae in *Lamellorthoceras* was also well illustrated by Mutvei (1956, pl. 1).

*Lamellorthoceras* has a straight or slightly cyrtconic conch that is circular in cross section. This genus is also characterized by sutures having broadly undulating saddles and lobes, as is also apparent in *Esopus sinuosum* (Pl. 1, fig. 7-9). Little is known about the shell surface of *L. vermiculare*, but on the surface of weathered specimens it can be seen that several individual lamellae converge adorally into a single lamella as they do in *Esopoceras* (compare Pl. 1, fig. 10,11 and Pl. 1, fig. 7-9).

Another similarity between *Lamellorthoceras* and *Esopoceras* is evident in the disposition of the cameral lamellae. Both radial and bilateral symmetry is apparent in *Lamellorthoceras* just as in *Esopoceras* (Pl. 2, fig. 2,3). A notable degree of similarity is evident in one thin section (Pl. 2, fig. 3), which shows the cameral lamellae of *L. vermiculare* becoming progressively curved at the ventral side near the siphuncle. We are not aware of any other genus that shows this feature. Another similarity of *Esopoceras* with *Lamellorthoceras* can be seen in *L. vermiculare* at the ventral side, where the lamellae converge or bend toward each other along a straight axis of symmetry (Pl. 1, fig. 10). This is comparable with the manner in which the lamellae of some of the specimens of *Esopoceras* have become

twisted along an axis of symmetry (Pl. 1, fig. 7-9). A degree of similarity is also noted in thin sections of *L. vermiculare* that shows the cameral lamellae becoming progressively curved toward the ventral side, whereas in another section they present a more radial aspect (Pl. 2, fig. 2,3).

A major difference between *Lamellorthoceras vermiculare* and *Esopoceras sinuosum* is in the position of the siphuncle and the shape and size of the conch. In *Esopoceras sinuosum*, the siphuncle is central, or only slightly subcentral, whereas in *Lamellorthoceras* it is quite eccentric. Also, the rate of expansion of the conch of *L. vermiculare* appears to be much greater than that of *Esopoceras* and it is much larger. As illustrated by Termier and Termier (1950) and by Teichert (1961), the siphuncle in the adapical portions of the conch of *Lamellorthoceras* lies close to the ventral side and is commonly accentuated by weathering. *L. vermiculare* displays some remnants of shell ornament that consists of circular or slightly oblique striae and lirae (Termier and Termier, 1950, pl. 135, fig. 8, 9; Teichert, 1961, pl. 2, fig. 1), whereas this type of ornament is unknown in *Esopoceras*.

Another species, *Lamellorthoceras gracile* (Termier & Termier, 1950, pl. 137, fig. 5, 6) was also reillustrated by Teichert (1961, pl. 2, fig. 11, 12), and this species is illustrated herein for comparison on Plate 1, figure 12. As described by Termier & Termier, *L. gracile* differs from *L. vermiculare* primarily in being more slender and in this respect it resembles *Esopoceras* more closely. It also differs slightly in age, *L. gracile* being slightly older (Siegenian) than *L. vermiculare* of Couvinian age. *L. gracile* has cameral lamellae that are not quite as sinuous as those of *Esopoceras sinuosum*, but it resembles *Esopoceras* in the bilaterally symmetrical arrangement of the cameral lamellae. In the New York species, the symmetry can be shown to be dependent on the orientation of the lamellae within the chamber. This may apply to both species of *Lamellorthoceras* as well as to species of some other genera.

The siphuncle of *Lamellorthoceras gracile* is highly eccentric (Pl. 1, fig. 12), and where it approaches the wall, it forms a cleft or depression that is enhanced by weathering. In *L. gracile* this feature is much more strongly developed than in the holotype of *Esopoceras sinuosum* where it

appears as a slight ?ventral depression only. In both *Lamellorthoceras* and *Esopoceras* the depression occurs only in the most distal camerae.

The chief differences between *Esopoceras* and *Lamellorthoceras* appear to be: 1) cross-sectional shape of the conch, circular in *Lamellorthoceras*, but slightly compressed to circular in *Esopoceras*; 2) details of the external edges of the lamellae, which tend to be more strongly twisted in *Esopoceras* than in *Lamellorthoceras*; 3) dimensions of the conch, which is much larger in *Lamellorthoceras*, particularly *L. vermiculare*, and also expands at a greater rate; 4) position of the siphuncle, which is more eccentric in *Lamellorthoceras*. Shell form in *Lamellorthoceras* varies from slightly cyrtconic to orthoconic. Only one known specimen (KUMIP 111626) of *Esopoceras* appears to be very slightly cyrtconic.

*Esopoceras* bears some resemblance to *Coralloceras* Zhuravleva (in Ruzhentsev, 1962), type species *Orthoceras coralliforme*, from the Couvinian of North Africa (Le Maitre, 1950). Although this species is comparable to *Esopoceras sinuosum* in having sinuous external edges of the lamellae as well as similar chamber dimensions, it differs in having a greater rate of conch expansion and in having straight, oblique sutures. Internally, *Coralloceras* differs markedly from *Esopoceras* in having fairly straight cameral lamellae which do not undulate or curve as do those of *Esopoceras*. The conch of *Coralloceras* is distinctly compressed dorsoventrally. *Coralloceras* has a characteristic ventral depression or fissure in the earliest camerae of some specimens. The appearance of this fissure seems to be related to a change in the position of the siphuncle from central to subcentral, but exact relationships are not known.

The genus *Arthrophyllum* Beyrich, 1850 (type species *Orthoceratites crassus* Roemer, 1843), known from France, Germany, and Turkey, was first regarded as a coral. Subsequently, *Orthoceras kahlebergense* Dahmer (1939) was assigned to *Arthrophyllum* (see Teichert, 1961). This genus also displays slightly sinuous lamellae on the surface of steinkerns but differs from *Lamellorthoceras* and *Esopoceras* in the disposition of the cameral deposits. Teichert (1961) noted that *Arthrophyllum* has simple radial cameral lamellae that are not as undulating or twisted as those of *Lamellorthoceras* and *Esopoceras*. Furthermore,



Teichert pointed out that in *Arthrophyllum* only episeptal deposits appear to be present and that these become progressively reduced in an anterior direction until they are altogether absent in the last few camerae. Such an arrangement of the cameral lamellae is not apparent in *Esopoceras*. One specimen of *Arthrophyllum* illustrated by Teichert (1961, pl. 1, fig. 7,8), shows radiating cameral lamellae that curve slightly toward the ventral side from a subcentral siphuncle. This particular specimen shows definite bilateral symmetry in the arrangement of the edges of the lamellae and in this respect bears much resemblance to *Lamellorthoceras* as well as *Esopoceras*. Schmidt (1956, p. 44) noted that *Arthrophyllum* has strongly folded cameral lamellae. Most species of *Arthrophyllum*, however, seem to possess straight cameral lamellae. *Arthrophyllum* also appears to differ from *Esopoceras* in a more eccentric position of the siphuncle, in greater rate of expansion of the conch, and in having shorter camerae.

The genus *Gorgonoceras* was described by Zhuravleva (1961) from the Couvinian of the Urals, with *G. visendum* as type species. It compares with *Esopoceras* in having nearly cylindrical phragmocones with a small angle of expansion and circular cross section. It also shows distinct bilateral internal symmetry and wavy cameral lamellae. Another notable similarity between *Gorgonoceras* and *Esopoceras* is the costulate shell surface, which bears distinct longitudinal ribs resembling the wall ornament in some specimens of *Esopoceras* (Pl. 2, fig. 6). Specimens of *Esopoceras* have similar but somewhat finer costules on what appears to be an inner wall layer. The arrangement of the cameral deposits in *Gorgonoceras* seems to be quite differ-

ent from that of *Esopoceras*. *Gorgonoceras* contains cameral deposits in the form of straight, thin, radiating lamellae with one large, more massive and distally bifid lamella occupying a ventral position. Also, the chambers of *Gorgonoceras* are slightly longer than those of the New York species.

Babin (1964) has evaluated the genera *Arthrophyllum*, *Lamellorthoceras*, *Coralloceras*, and *Gorgonoceras* and presented reasons for considering at least three of these, *Arthrophyllum*, *Lamellorthoceras*, and *Coralloceras*, to be congeneric. He reviewed the various internal and external features used to distinguish these genera and pointed out that many of their features are shared by all of them. This appears to be especially true for *Arthrophyllum* and *Lamellorthoceras*, which share many characteristics as previously discussed by Teichert (1961). However, on the basis of differences in cameral deposits, we are inclined to regard these as separate genera, although we concede that reasons could be cited for regarding all of them as subgenera of *Arthrophyllum*.

The characteristics of all five genera are compiled in Table 1 from which it can be seen that many features and characteristics are indeed shared by different genera, and some features of *Esopoceras* are shared by the previously known genera. It is also apparent from the foregoing discussions, as well as from the data presented in Table 1, that considerable variations are present in all five genera. This is especially true for the position of the siphuncle, sutures, length/width ratios of camerae, and apical angles, but probably also for the internal arrangement and disposition of the cameral lamellae.

## SUMMARY

We consider the disposition and arrangement of the cameral deposits to be of paramount importance in differentiation at the specific as well as the generic level. We have demonstrated that in many specimens of *Esopoceras* cameral deposits show intricate and complex arrangements, which are difficult to ascertain without careful thin section study. Furthermore, it has been

pointed out that in *Esopoceras* there is considerable variation not only within the camerae but also in other characteristics such as the shape of the conch, length/width ratio of camerae, and the external expression of the lamellae. Such variations pose considerable difficulties in taxonomic evaluations at the generic and specific levels.

In cross sections, the cameral lamellae of *Esopoceras* appear either straight or highly sinuous and curved, depending on the position of the section within a camera (Pl. 1, fig. 3; Pl. 2, fig. 4,7). A similar arrangement is apparent in *Lamellorthoceras* (Pl. 1, fig. 8,9). Arrangements of the cameral lamellae in the other genera of Lamellorthoceratidae are not known in the same detail, although the variations noted in Table 1 may be attributable to internal complexities of the cameral deposits. We believe that, in order to properly evaluate the taxonomic positions of the known genera and species, a detailed study of the cameral deposits would be required.

The five genera of the family Lamellorthoceratidae can be divided into two groups based on the development of episeptal and hyposeptal deposits and on the complexity and symmetry of external lamellae, expressed on the surface of steinkerns. Both *Arthrophyllum* and *Corallocceras* have fairly straight cameral lamellae, which appear as episeptal deposits only. *Lamellorthoceras*, *Gorgonoceras*, and *Esopoceras* on the other hand have both episeptal and hyposeptal deposits that are undulatory (Table 1). *Lamellorthoceras* and *Esopoceras* have broadly undulating suture patterns and have external lamellae that curve around a longitudinal axis producing pronounced bilateral symmetry. *Esopoceras* differs in having

a greater degree of curvature, reflecting a correspondingly greater degree of internal cameral complexity. In *Gorgonoceras*, bilateral symmetry is produced in quite another way. Here, although the cameral lamellae are wavy and undulating as in the other two genera, they are not curved about a longitudinal axis and are not folded appreciably. Instead, *Gorgonoceras* has a thick bifid cameral lamella in a ventral position.

Assuming the function of the cameral deposits to be hydrostatic, the arrangements in all three genera could have achieved similar results in stabilizing or balancing the conch by weighting the shell along a ventral axis. A diagrammatic reconstruction of the arrangement of the camera deposits in *Esopoceras* is presented (Fig. 2).

Considering the extreme complexity of these deposits, it seems that they must have been secreted by mantle tissue in the camerae. Details of such a discussion are outside the scope of this paper and the reader is referred to Flower (1955), Zhuravleva (1961), Teichert *et al.* (1964) and Fischer and Teichert (1969) for a discussion of cameral deposits and their origin. The means by which the organism accomplished the formation of these complex systems of cameral lamellae is a pressing problem and one on which the lamellorthoceratids may shed more light.

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# EXPLANATION OF PLATES

## PLATE 1

### FIGURE

- 1-9. *Esopoceras sinuosum* Stanley & Teichert, n. sp., Lower Devonian, New York.—1. Lateral view of single camera showing twisted outer edges of cameral lamellae, exposed through partial weathering of shell wall,  $\times 2$ . KUMIP 111634.—2. Same specimen, septal view with near central siphuncle,  $\times 2$ .—3. Slightly oblique view showing sinuous outer edges of cameral lamellae; small fragment of succeeding septum present,  $\times 3$ . KUMIP 111626.—4. Photomicrograph of a polished, slightly tangential cross section of specimen illustrated in Pl. 2, fig. 6; section is at periphery of shell and shows the terminal, bifurcating loops of the cameral lamellae as they meet the wall; darker projections are portions of the longitudinal costules of the inner wall,  $\times 50$ . KUMIP 111623.—5. External view of specimen with faint annulations of the surface,  $\times 2$ . KUMIP 111632.—6. Transverse view of holotype, showing slightly subcentral siphuncle and radiating lamellae which curve toward one side,  $\times 2$ . KUMIP 111622.—7. Lateral view showing sinuous lamellae of surface of steinkern of N.Y. sp.,  $\times 2$ . KUMIP 111624.—8. Clay impression of specimen fig. 7, showing how the lamellae become progressively twisted toward a central axis (dashed line). Some overlap present,  $\times 2$ .—9. Lateral view of same specimen showing side opposite that shown in fig. 7; posterior region partially weathered; note lamellae becoming progressively straighter from left to right. Position of sutures match with those of adjacent specimens in figs. 7 and 9,  $\times 2$ .
- 10,11. *Lamellorthoceras vermiculare* Termier and Termier.—10. Ventral view, Couvinian, Morocco,  $\times 2$ . Specimen D8162 figured by Termier and Termier, 1950, pl. 138, fig. 1, and by Teichert, 1961, pl. 2, fig. 10.—11. Dorsal view,  $\times 2$ . Specimen figured by Termier and Termier, 1950, plate 135, fig. 11.
12. *Lamellorthoceras gracile* Termier and Termier, ventral view, Siegenian, Morocco. Portion of

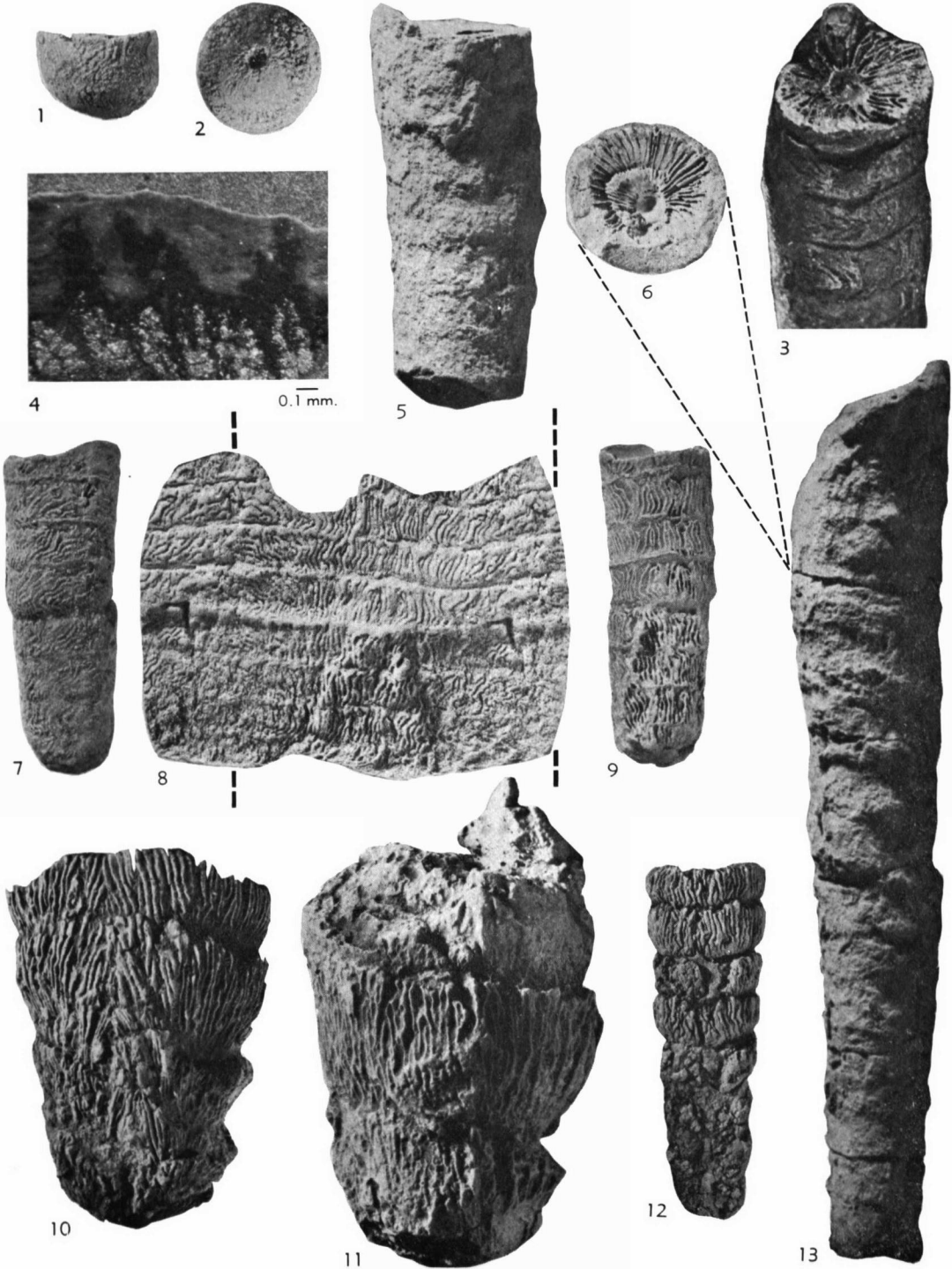
siphuncle excavated through weathering of conch,  $\times 2$ . Specimen Di831a figured by Termier and Termier, 1950, pl. 137, fig. 5, and by Teichert, 1961, pl. 2, fig. 12.

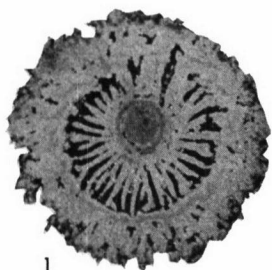
13. *Esopoceras sinuosum* Stanley & Teichert, n. gen., n. sp. Holotype, consisting of 16 camerae,  $\times 2$ . KUMIP 111622.

## PLATE 2

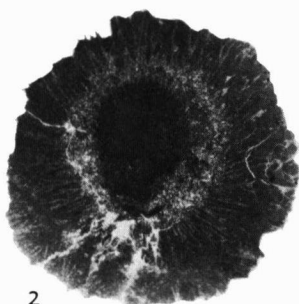
### FIGURE

- 1,4-9. *Esopoceras sinuosum* Stanley & Teichert, n. gen., n. sp., Lower Devonian, New York.—1. Cross section through a camera showing near central siphuncle and radially symmetrical lamellae,  $\times 4.5$ .—4. Same specimen as Fig. 1, ground slightly farther into next chamber; note curved lamellae and bilateral symmetry,  $\times 4.5$ .—5. Cross section of specimen from upper left region of which photomicrograph figure 5 is taken,  $\times 4.5$ . KUMIP 111630.—6. Portion of phragmocone showing longitudinal costules of surface,  $\times 3.4$ . KUMIP 111623.—7. Polished cross section showing radiating cameral lamellae becoming curved toward the ?dorsal side; siphuncle not apparent,  $\times 4.5$ . KUMIP 111633.—8. Photomicrograph of cross section in which cameral lamellae meet the wall; note looped and curved nature of lamellae; specimen mostly replaced by pyrite. KUMIP 111633.—9. Photomicrograph cross section, showing distinct double-layered nature of lamellae. KUMIP 111630.
- 2,3. *Lamellorthoceras vermiculare* Termier & Termier, Middle Devonian (Couvinian), North Africa.—2. Cross section; note branching lamellae and radial symmetry,  $\times 1.9$ . Specimen DM 8155b, figured by Termier and Termier, 1950, pl. 135, fig. 13, and by Teichert, 1961, pl. 1, fig. 12.—3. Cross section; note the cameral lamellae on the ?ventral side which become curved in that direction producing bilateral symmetry,  $\times 3.4$ . Specimen DM 8155a, figured by Termier and Termier, 1950, pl. 135, fig. 12, and by Teichert, 1961, pl. 1, fig. 11.

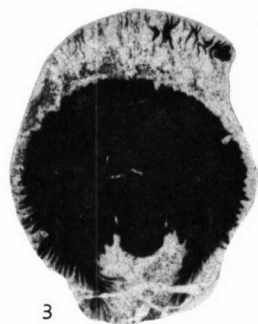




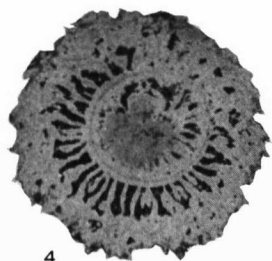
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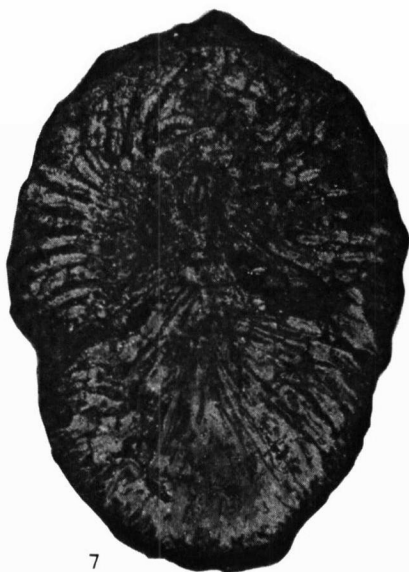
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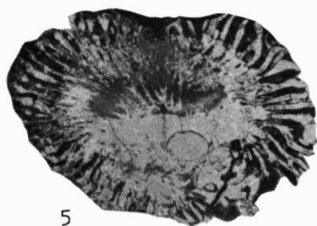
4



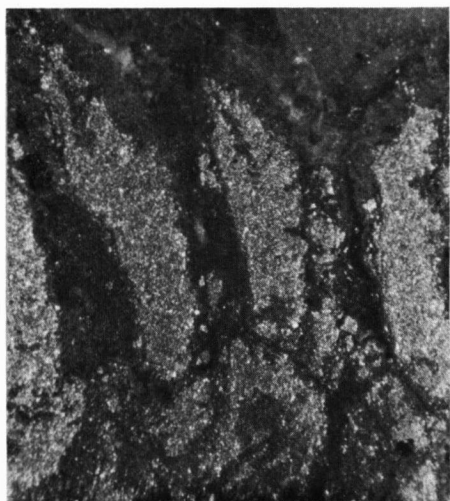
6



7

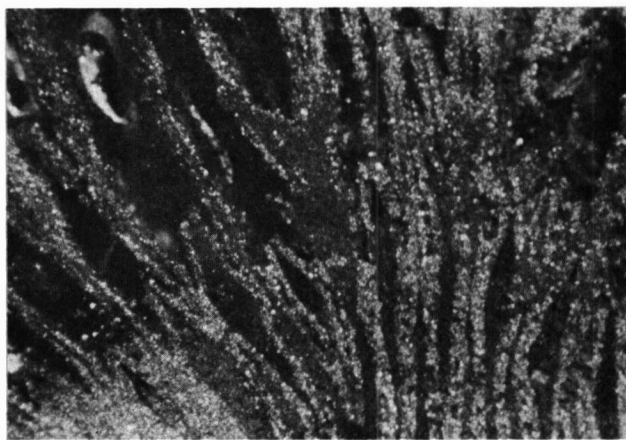


5



8

0.1 mm.



9

0.1 mm.